

Auditory atavism and integrated pathways for hearing in snakes

Bruce A. Young

Abstract. Although the auditory sensitivity range of snakes is limited, snake hearing may not be as restricted as previously thought. Three (non-exclusive) hypotheses for the ophidian auditory frequency response are advanced herein: fluid dampening, impedance matching, and neural physiology.

There are now multiple physiological and behavioral studies demonstrating that snakes can respond to vibrational stimuli in the air, ground, or even water (e.g., Westhoff et al., 2005; Young, 2003, 2005). Two earlier physiological studies reported the auditory frequency responses of snakes; while the ranges were similar, the values reported by Hartline (1971a, 1971b) were more restricted than those reported by Wever (1978). These differences may reflect the underlying methodological approaches: Hartline used intracellular recordings while Wever relied on cochlear microphonics, a technique that has been criticized as potentially over-representing auditory ranges (e.g., Manley, 1990).

Young and Harris (ms sub) presented rattlesnakes airborne stimuli of different frequency and amplitude combinations, and reported numerous positive responses beyond the auditory range described by either Hartline (1971a, 1971b) or Wever (1978). These results suggest that snake hearing may not be as restricted as previously thought; nevertheless, the auditory sensitivity range of snakes (from approximately 50 — 1,000 Hertz) is limited, even when compared to other squamate reptiles (Wever, 1978).

A proximate explanation for the restricted auditory range of snakes has never been developed. Herein I will advance three (non-exclusive) hypotheses for the ophidian auditory frequency response; fluid dampening, impedance matching, and neural physiology. In the mammalian auditory system the displacements of the stapes at the oval window create pressure waves within the perilymphatic fluid that course through the bony labyrinth, around the helicotrema, and ultimately are dissipated through the round window into the middle ear cavity. In the

ophidian auditory system the middle ear cavity is reduced to a small space immediately surrounding the stapes (Wever, 1978) or is lost completely, and there is no round window. As a result, pressure waves within the perilymphatic fluid essentially deflect off of the back of the bony labyrinth, change direction, and radiate back towards the stapedia footplate. Wever (1978) termed this unusual perilymphatic circulation pattern the reentrant fluid circuit.

These perilymphatic pressure waves are ultimately dissipated at the pericapsular sinus, a membranous extension off the bony labyrinth that surrounds the stapedia footplate and the proximal portion of the body of the stapes. Depending on the exact shape and size of the cochlea (see Miller, 1968) some frequencies of perilymphatic pressure waves may reach the pericapsular sinus at significant enough amplitude to effectively dampen the displacements of the stapes, thereby reducing the auditory range of the snake. A model of the stapedia displacements and resulting fluid mechanics within the cochlea (e.g., Ruggero and Temchin, 2002; Gan et al., 2004) could determine what impact, if any, the reentrant fluid circuit has on frequency range.

The most commonly cited model for vibration detection in snakes, what Wever (1978) described as the “substrate hypothesis,” posits that groundborne vibrations are received and transmitted by the lower jaw and its suspensory system. In order for an external vibration to be converted into a perilymphatic pressure wave in this fashion, the displacements would have to travel through the following structures: the scalation of the lower jaw, the underlying connective tissue, the bones (and joints) of the lower jaw, the quadrate/articular joint, the long axis of the quadrate, the quadrate/extrastapes joint, the long axis of the extrastapes, the extrastapes/stapes joint, and finally the long axis of the stapes. The biomechanical properties of each link in this transmission chain could impact the

frequency and/or amplitude of the vibratory wave.

Since impedance matching is frequency sensitive, an impedance mismatch between the ground-borne vibration and any link in this chain could differentially impact certain frequencies resulting in the narrow auditory range of snakes. Wever and Vernon (1960) and Wever (1978) provided some evidence for impedance matching by stimulating different component parts directly, however the details of vibrational transmission through this functional chain have never been explored. It may be particularly profitable to examine the relationship between auditory sensitivity range and the morphology of the contact between the stapes and the quadrate. There is significant morphological variation in this region, including the number of intervening cartilaginous bodies (the extrastapes), the area of contact, and the extent of connective tissue sheathing between the two bones (e.g., de Beer, 1937; Kamal and Hammouda, 1965; Wever, 1978; Rieppel, 1980). The limited data presented by Wever (1978) suggest that species with a more "open" stapes/quadrate joint also have lower auditory sensitivities and more restricted frequency ranges. The impact of impedance matching could also be placed in a broader context by looking at hearing performance within other squamate taxa that include forms with and without tympanic membranes (Mertens, 1971; Wever, 1978) or forms in which the tympanic membrane has been occluded by the scalation (e.g., *Tympanocryptis*).

Hartline (1971a, 1971b) reported that the latency and refractory periods of mid-brain auditory neurons were significantly slower than those of other terrestrial vertebrates. In fact, the cellular performance of these neurons was divergent enough that Hartline questioned whether snakes could process vibrational information in a behaviorally relevant way. Since Hartline was recording from the mid-brain of the snake, the physiological properties he quantified could have arisen at either a peripheral receptor (a cochlear hair cell), a relay neuron (such as the Nucleus Magnocellularis), or within the auditory mid-brain itself. Furthermore, these unusual temporal properties could be produced within a single neuron (presumably by differences in gated channel proteins) or through the interaction of multiple neurons (perhaps by differences in post-synaptic receptors).

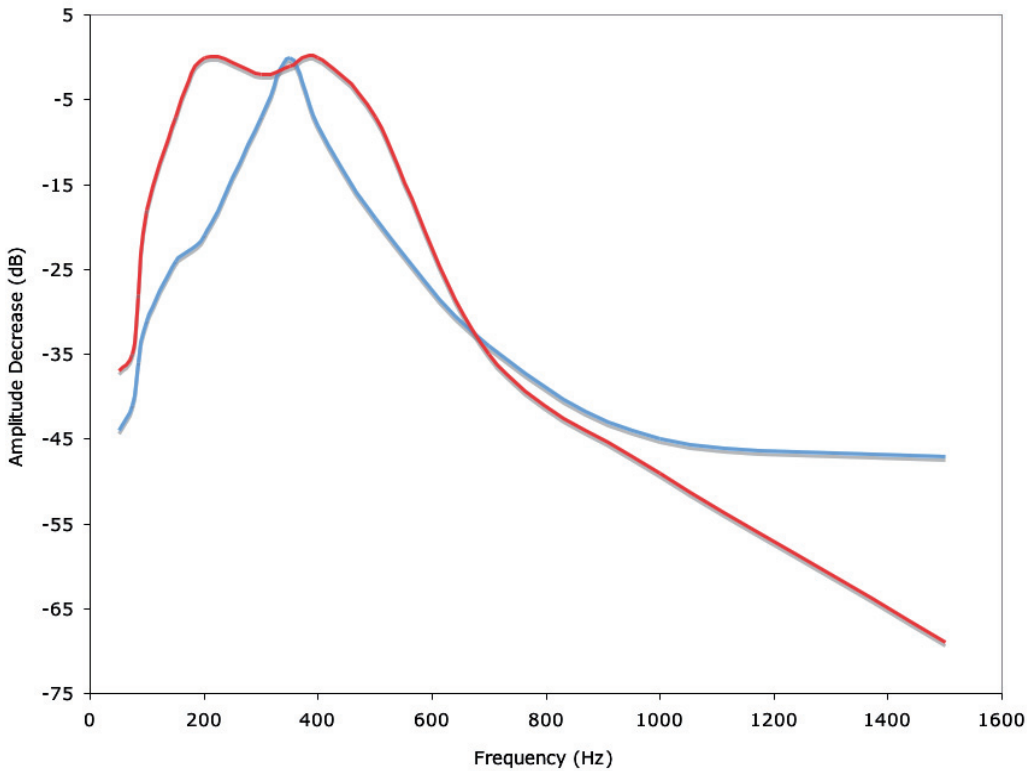
In theory at least, these same functional attributes

could affect frequency response as well as temporal response. The same neural physiology that led Hartline to question the behavioral significance of vibratory stimuli to snakes could also limit the frequency range of the auditory response. Could the narrower frequency range reported by Hartline (1971a, 1971b), as compared to Wever (1978), simply reflect the fact that Hartline was recording from higher up in the auditory system, and thus found additive influences from the additional neurons? It would be informative to obtain intracellular recordings from the basilar papilla and to compare these to both Wever's (1978) cochlear data and Hartline's (1971) mid-brain data.

In addition to these three (non-exclusive) proximate hypotheses, it may be informative to examine the auditory range of snakes from a broader (ultimate) perspective. The phylogeny of snakes remains uncertain. The classic scenario for the evolution of snakes, often referred to as the "fossorial theory," proposes that snakes evolved through a fossorial phase, leading to reduction then loss of the limbs, loss of the external ear, and degeneration off the eye (e.g., Walls, 1942). This scenario has been challenged by workers who have argued for an aquatic ancestral environment (e.g. Lee and Caldwell, 2000). The fossorial theory is relevant to snake hearing not only in accounting for the loss of the external ear, but perhaps also by explaining the restricted auditory range.

Sandy soils propagate vibrations best over a rather narrow range of frequencies centered around 300 Hertz (e.g., Aicher and Tautz, 1990); indeed, the frequency profiles for vibratory propagation in soil and auditory reception in snakes are very similar (Fig. 1). Interpreted this way, the frequency response range of the snake's ear may be a form of auditory atavism, where the modern physiological performance reflects a specialization for ancestral environmental conditions. Some snake species are semi-fossorial in sandy soils (e.g., *Eryx*, *Cerastes*) while other species are found on the surface of the sand (e.g., *Psammodon*). But there are many arboreal, semi-aquatic, and aquatic species — as well as numerous terrestrial forms that routinely adopt postures in which the lower jaws are held off the surface of the substrate (e.g., *Trimorphodon*) — for which this potentially ancestral frequency range may not be optimal for their ecological interactions.

Figure 1. Comparison of the frequency profiles of vibration in damp sand (light trace, data taken from Aicher and Tautz, 1990) and the frequency response of a garter snake (dark trace, data taken from Wever, 1978).



Formulating proximate and/or ultimate explanations for the auditory specializations in snakes is hampered by our incomplete understanding of the basic mechanics of this system. Wever and Vernon (1960) demonstrated conclusively that the ophidian cochlea is capable of responding to both airborne and groundborne vibrations; Hartline (1971b) extended these findings by showing that snakes can also detect vibrations from their body surface. In addition to these auditory and somatic systems, there are several types of cutaneous sense organs in snakes that appear capable of responding to vibrational information (e.g., Proske, 1969; Jackson and Doetsch, 1977; Povel and Kooij, 1997).

Maps of the response field(s) at the level of the auditory mid-brain (Hartline, 1971b) suggest that there are multiple pathways for hearing in snakes, at least up to this level of the auditory processing. When identical vibrational cues were presented to rattlesnakes as either groundborne or airborne stimuli, the rattlesnakes showed significant differences in latency time to response, orientation reaction, and

relative strength of response to different stimuli, suggesting that vibrational stimuli from these two different sources were being processed differently (Young, 2004).

The presence of multiple, at least partially independent, pathways for hearing means that the ophidian auditory system may be one of the most specialized among terrestrial vertebrates. Until we know more about the basic mechanics of these different sensory pathways, and their integration, we can not explore the possible phylogenetic and ecological specializations of this system. For example, what cutaneous receptors are responsible for “somatic” hearing? How are these receptors distributed over the body of the snake, and does this distribution differ between arboreal and aquatic species, or among different phylogenetic groups? Understanding the functional integration of the ophidian auditory system may provide insights into the phylogeny of snakes, as well as their subsequent ecological divergence.

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